THE STATUS OF SOME AMERICAN SPECIES OF MYRIOPHYLLUM AS REVEALED BY THE DISCOVERY OF INTERGRADE MATERIAL BETWEEN M. EXALBESCENS FERN. AND M. SPICATUM L. IN NEW JERSEY

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This paper arises out of a coöperative project between the Forests and Parks Section of the New Jersey Department of Conservation and Economic Development and the Botany Department at Rutgers University, the State University of New Jersey. The project was initiated in order to study the ecology and life history of a dominant aquatic weed in several lakes of northern New Jersey and to suggest, if possible, intelligent control procedures. This weed has been identified for Lake Musconetcong as *Myriophyllum exalbescens* Fern. (Renlund 1950, p. 169).

The present study was undertaken when the writer noted that although the plants in Lake Musconetcong keyed readily to *M. exalbescens* in the eastern manuals (Fassett 1940, Muenscher 1944, Fernald 1950 and Gleason 1952), they did not conform strictly to the descriptions of this species. This material has a greater number of capillary leaf divisions than does *M. exalbescens* and displays a decided protrusion of the lowermost floral bracts beyond the fruits. Fernald (1919) had used both of these characters to separate *M. exalbescens* from *M. spicatum* L. (1753) in his original description of the former:

> . . . aquatic herb; the stem glabrous, leafy, simple or branching, purple, in the dried state becoming white: leaves verticillate, rarely in 3's, commonly in 4's, 1.2–3.0 cm. long, with 7–11 pairs of capillary flaccid or barely a little rigid segments [this range later became 6–11 pairs: Fernald 1950, p. 1073]: spikes terminal, almost naked, the flowers verticillate; the lower pistillate, the upper staminate, sessile: bracts rarely equalling the fruit, spatulate-obovate or oblong-cochleiform; the lower serrate, the upper entire: bracteoles ovate, entire, brown-margined, 0.7–1.0 mm. long; petals oblong-obovate, concave, 2.5 mm. long: stamens 8; anthers oblong, 1.2–1.8 mm. long: fruits subglobose, very slenderly 4-sulcate, 2.3–3.0 mm. long; the merocarps rounded on the back, smooth or rugulose.

According to Fernald, "*M. exalbescens* [had] always passed in America as *M. spicatum* L. The latter species of Eurasia, however, differs from the American plant in several characters:

the principal leaves of the primary stems have 14–21 pairs of rigid slenderly linear divisions; the bracts are rhombic-obovate; the bractlets are suborbicular or reniform, broader than long, and distinctly shorter than in most of *M. exalbescens*, 0.5–0.8 mm. long; and the linear anthers tend to be longer, being 1.8–2.2 mm. in length. In *M. exalbescens*, furthermore, the dried stems very strongly tend to become white, although this change is not always noted; in *M. spicatum*, however, the old herbarium specimens still retain a fulvous or olivaceous tone in the stems."

Concerning the floral bracts, Fernald (1919, p. 123) implies that they only occasionally exceed the fruits in some varieties of *M. spicatum*. Hegi (1926, p. 901), however, states that they are typically as long as or exceeding the flowers. This would appear, therefore, to be an additional valid character upon which to separate the two species.

As a further point of separation, Hultén (1947, pp. 1159–1160) stated that winter buds never develop in *M. spicatum* while such buds are often prominent in *M. exalbescens*.

A summary of the published differences between these two species is provided on Table I.

TABLE I

Comparison of characters used to separate *M. exalbescens* from *M. spicatum* in Series I and Series II material from New Jersey

Character	*M. spicatum*	*M. exalbescens*	*Series I*	*Series II*
1—shape of floral bracts	rhombic-obovate to elongate	spatulate-ovate or oblong-cochleiform	ovate to elongate	spatulate-ovate
2—relative length female bracts	longer than fruits	rarely equalling fruits	exceeding fruits	rarely equalling and never exceeding fruits
3—shape of bracteoles	suborbicular or reniform	ovate	ovate	ovate
4—dimensions of bracteoles	broader than long	longer than broad	both	both
5—dried stem color	olivaceous or fulvous	whitened	whitened to olivaceous	whitened to fulvous
6—winter buds	absent	present	reduced	present
7—number of pairs of leaf divisions	14–21	6–11	7–20	4–12
8—length of bracteoles	0.5–0.8 mm.	0.7–1.0 mm.	♂: 0.5–1.2 ♀: 0.6–1.0	♂: 0.5–1.3 ♀: 0.7–1.1
9—length of anthers	1.8–2.2 mm.	1.2–1.8 mm.	0.9–2.1 mm.	1.2–2.0 mm.

In the same paper containing the description of *M. exalbescens*, Fernald also described *M. magdalense* (later corrected to *M. magdalenense:* Fernald 1924). This species very closely resembled *M. exalbescens* except for the possession of "fruit so very unlike that of the latter species or of the old world *M. spicatum*." This appears dubious since "the material of *M. magdalense* [was] mostly immature, only one plant being found with good fruit," and two other species, *M. exalbescens* and *M. verticillatum* var. *intermedium* Koch, were present in the vicinity so that the possibility of hybridization was genuinely extant. *M. magdalenense* was described as follows:

> Similar to *M. exalbescens*; the stem branching, becoming white when dried: leaves mostly in 4's, 1–2 cm. long, with 3–7 pairs of capillary flaccid segments 0.5–1.3 cm. long; the upper emergent ones elongate-oblanceolate or linear, short-pectinate or subentire: spikes terminal, with the rachis filiform; flowers verticillate, the lower pistillate, the upper staminate, sessile: bracts elongate, linear oblanceolate, conduplicate, up-curved at the end, entire or the lower pectinate, 0.3–1 cm. long: bractlets ovate, 0.6–0.8 mm. long: petals ovate-oblong, concave, 1.5 mm. long: stamens 8; anthers oblong, 1.5 mm. long (immature); fruits subglobose, 3 mm. long, very broadly 4-sulcate; the merocarps with rounded rugose backs.

Chapman (1889, p. 143) cited the description of a Floridian species, *M. laxum* Shuttl., which is obviously very closely related to the two species of Fernald:

> . . . stem long, slender; leaves four in a whorl; the floral ones reduced to minute nearly spatulate bracts, shorter than the flowers, which thus formed an interrupted almost naked spike; fruit roughened with minute warts, with the lobes obtuse.

Small (1933, pp. 954–955) supplies additional information on this species:

> Stamens 8; corolla deciduous. Leaves in 4's; blades of the approximate submersed ones with 3–7 pairs of capillary segments; those of the floral ones spatulate; petals elliptic, 2.3–3.0 mm. long; anthers linear to narrowly elliptic, about as long as the filaments; fruit ovoid-globose, about 1.5 mm. long; carpels minutely warty.

In addition, Grout (1896, p. 11) described the bractlets as small, lanceolate and hyaline.

From a careful comparison of these descriptions, it would appear that these four species are closely related as a single complex whose geographic segments have differentiated in very small degrees along different pathways away from the common stock. The question arising is whether or not these segments

have achieved "truly" specific status. It is the purpose of the subsequent sections of this paper to provide an answer to this question for *M. exalbescens* through a comparison of material from New Jersey coupled with the use of herbarium and literature resources.

Two series of collections from various locations in New Jersey were made. Series I contained specimens resembling the material of Lake Musconetcong in having a large number of leaf divisions and the lowermost floral bracts exceeding the fruits. Series II comprised more typical *M. exalbescens* in having shorter bracts and fewer leaf segments. The Series I material was collected at the following locations: 1) A fertile population from Lake Musconetcong, Morris and Sussex Counties. 2) Lake Lakawanna, several miles northwest of Lake Musconetcong in Sussex County; fertile. 3) The Delaware and Raritan Canal, Middlesex County; fertile. 4) Johnson Park Pond (Upper), several hundred yards from the third site; fertile. Series II material was collected from 1) Gardner's Pond, Sussex County; fertile. 2) Wolf Lake, less than a mile above Lake Lackawanna; sterile. 3) Wright's Pond, located above and connecting with Wolf Lake; sterile. Of interest is the fact that the latter two locations flow into Lake Lackawanna, yet this lake has only Series I material represented. The material which was sterile was grouped into Series II on the basis of the small number of leaf divisions alone since floral bracts were lacking.

There are only two additional species of *Myriophyllum* known to the writer in the Sussex-Morris County area from which most of the above collections were made. *M. heterophyllum* Michx. is very widespread. The material from Wolf Lake and Wright's Pond can be separated from it in the sterile condition, even though the number of leaf divisions is similar, by the whitened stems and the large winter buds of the former. *M. verticillatum* (var. *pectinatum* Wallr.) is represented by a single sterile population inhabiting the shallow ecotonal waters of a cove in Lake Musconetcong.

Using the qualitative and quantitative premises for the separation of *M. exalbescens* from *M. spicatum* (Table I), the two New Jersey series were carefully compared. Quantitative

information was obtained by counting or measuring random samples of each of the structures indicated. The frequency distributions obtained by so-doing were subjected to statistical analyses to determine the degree of significance of any differences observed between means of the two series. Table I compares the results and Table II provides a summary of the statistical findings. In the discussion following, each character is numbered to correspond with similar numbers in the tables to facilitate reference by the reader.

TABLE II

Summary of statistical analyses of quantitative characters in Series I and Series II material

Series	*n*	*r*	*M*	σ	$\sigma/\sqrt{n}$	D/E_d	t_5
			7—Number of pairs of leaf divisions				
I	538	7–20	14.94	11.66	0.50	7.034	1.95996
II	592	4–12	8.23	10.10	0.41		
			8a—Length of male bracteoles (mm.)				
I	91	0.5–1.2	0.964	3.03	0.32	0.016	1.95996
II	60	0.5–1.3	0.978	3.56	0.46		
			8b—Length of female bracteoles (mm.)				
I	90	0.6–1.0	0.889	3.32	0.35	0.025	1.95996
II	72	0.7–1.1	0.913	4.62	0.54		
			9—Length of anthers (mm.)				
I	576	0.9–2.1	1.70	12.10	0.50	0.048	1.95996
II	142	1.2–2.0	1.65	6.97	0.58		

n equals the number of variates included in each sample; r is the range in the magnitude of each character; M is the mean of each character as calculated by the assumed mean method; σ is the standard deviation; $\sigma/\sqrt{n}$ is the standard error; t_5 signifies Fisher's t-value at 5% probability (see any statistics text for a table of t); D is the difference between the means of the two series; E_d is the standard error of this difference (calculated from the expression $E_d = \sqrt{\sigma/\sqrt{n_1} + \sigma/\sqrt{n_2}}$). If D/E_d exceeds t_5, the observed differences between the means of the two samples are significant. Such is the case only in the comparison of number of pairs of leaf divisions in the two series.

1. *Shape of floral leaves.* The uppermost (staminate) bracts were similar in both series: spatulate, both ovate and obovate; margins usually denticulate but often entire. The lowermost (pistillate) bracts differed: elongate and serrate to completely pinnate in Series I; spatulate-ovate and serrate in Series II. No rhombic contours were encountered.

2. *Relative length of lowermost bracts.* Almost always exceeding the fruits in Series I; rarely equalling and never exceeding the fruits in Series II.

3. *Shape of bractlets.* Ovate in both series.

4. *Dimensions of bractlets.* Some were broader than long and others were longer than broad in both series.

5. *Dried stem color.* Examination of sheets at the New York Botanical Gardens indicated this character to be of little utility to the average observer. There was free intergradation of stem color in both American and continental material. The dried stems of Series I material are whitened to olivaceous; those of Series II whitened to fulvous.

6. *Winter buds.* Turions are very prominent in Series II material, obtaining several centimeters or more in length. They are present in Series I specimens but are very much smaller, being usually only a centimeter or less. Futhermore, those of Series I are bright red through stramineous to light green whereas those of Series II are deep green.

7. *Number of pairs of capillary leaf segments.* The sheets at the New York Botanical Gardens supported Fernald's contention that *M. exalbescens* possessed fewer pairs of leaf divisions than *M. spicatum.* American material had 5–12 pairs and Eurasian 10–21 pairs, with the exception of that from Scandinavia and a single specimen from the Soviet Union which resembled American specimens more in this regard. The Series I plants had 7–20 pairs of divisions with a mean of nearly 15; the Series II material had only 4–12 pairs with a mean of 8.23. The analysis (Table II) indicated these differences to be significant: D/E_d was greater than t_5. This significance was at less than one per cent probability indicating that less than one variate in one-hundred from either series would intergrade with those from the other series.

8. *Length of bracteoles.* Although Fernald did not treat separately the bractlets of the two sexes, this was done here to eliminate that factor as a source of variability. None of the differences was significant. There was, however, a non-significant degree of sexual dimorphism in both series, the male bractlets being somewhat longer than those of the pistillate flowers.

9. *Anther length.* No significant differences existed between the means of the two series.

Reference to Table I allows ready comparison of the results outlined above with the published descriptions of the same characters for *M. spicatum* and *M. exalbescens.* Both series of New Jersey material are seen to intergrade between the two species. Although a specific character may be skewed in the direction of one of the species, it is generally influenced by the other. For example, the bracteoles of *M. spicatum* are described as shorter than those of *M. exalbescens*, and although the Series I bracteoles are insignificantly shorter than those of Series II, the degree is less than described.

Thus both series display an admixture of characteristics from both species, and although Series I leans more toward *M. spicatum* and Series II the opposite, the conclusion must be that none of the New Jersey material sampled is strictly either of the described species.

Three possibilities exist by which to explain the status of this New Jersey material:

1. *That the indigenous M. exalbescens hybridizaed with another indigen to produce a similitude to M. spicatum.* Although the potential for this occurrence is extant in the presence of *M. heterophyllum* and *M. verticillatum*, the writer is of the opinion that the production of a hybrid so closely resembling an existing species from another continent is clearly beyond probability. However, it should be mentioned that *M. verticillatum* is a highly variable circumboreal species so that many present species, including *M. spicatum* and *M. exalbescens*, could actually be well-differentiated varieties of a vast *M. verticillatum* complex. Indeed, Gmelin believed *M. verticillatum* and *M. spicatum* to be one and the same species, and Perrot (1900) provided a degree of anatomical evidence which supported this view (p. 202). The writer shares this point of view. After flowering of the Series I material in Lake Musconetcong the lowermost floral bracts often grow outward and, in basipetal succession, assume the fully-dissected character of normal submerged leaves or of the pinnately-divided floral leaves of *M. verticillatum*. It is therefore possible that the Series I plants are actually derived from *M. verticillatum* or a combination of this species with *M. exalbescens*. Since, however, conclusive evidence in support of such broad considerations is lacking, this hypothesis must be regarded as the least valid of the three possibilities.

2. *That M. spicatum became introduced and intergraded with the indigenous M. exalbescens.* Lake Musconetcong was originally impounded eleven decades ago to supply water for the trans-state Morris Canal. There existed at one time direct connection between canal and lake. This canal and the Delaware and Raritan Canal in central New Jersey were both used in the transportation of goods, probably including continental imports, across the state. Thus there existed in previous time two possible sites of introduction of *M. spicatum* from Eurasia. There is, however, no proof to support this hypothesis and the following evidence tends to negate it. The *M. spicatum*-like Series I plants are not widespread in the Delaware and Raritan Canal occurring, to the author's knowledge, only at the collection site. The Morris Canal is now abandoned, only discontinuous seg-

ments of it remaining submerged. Of these areas only one, into which Lake Musconetcong flows directly, is known to contain a sparse population of Series I material. Thus if *M. spicatum* *was* introduced into either of the canals, it did not there meet with the widespread success characteristic of the Series I plants in other sites where it occurs.

3. *That the New Jersey material represents intergrades between geographically disjunct segments of a circumboreal M. spicatum-M. exalbescens complex.* The distribution of such a complex is depicted roughly in Figure 1. Under this hypothesis two possibilities prevail: 1) that complete separation of the two species was never achieved and that intergrades exist at the peripheries of the overlapping ranges, or 2) that subsequent to complete disjunction (which permitted the differentiation of Eurasian and American populations) reunion was achieved and intergrade material resulted. The latter is similar to hypothesis number two above, only broader in aspect. The writer favors hypothesis number three because of the following direct and indirect evidences.

Since Fernald's separation of *M. exalbescens* from the complex, various American investigators working in various regions have failed to recognize it either through unfamiliarity or because their material would not permit them to do so. House (1924), working in New York, listed the species of that region as *M. spicatum*, making only casual note of Fernald's synonymy. Wiegand and Eames (1925), however, working in the Cayuga Lake Basin, did recognize the distinction. Jepson (1925), working with limited collections from California, assigned Fernald's species to the varietal status, *M. spicatum* var. *exalbescens* Jeps. Other western workers, Peck (1941) in Oregon and Kearney and Peebles (1942) in Arizona, recognized *M. exalbescens* and merely mentioned the synonymy of Jepson. Tidestrom (1925) in Utah and Nevada, Tidestrom and Kittell (1941) in Arizona and New Mexico, Pepoon (1927) in Illinois, and Rydberg (1932) in the Plains and Prairie regions all list *M. spicatum* for their respective regions. They do not, however, list synonymy. Deam (1940) listed *M. exalbescens* for Indiana. Standley (in Cooper 1930) referred Alaskan material to *M. spicatum*. Hultén (1947), also working in the Alaskan region, assigned *M. exal-*

Figure 1. Condensed equal area sinusoidal projection of the world. The land areas which are unblacked represent the approximate range of the *M. spicatum-M. exalbescens* complex after Fernald 1919, 1950, Hegi 1926 and Hultén 1947. Hultén cites the occurrence of *M. spicatum* in South America and Australia whereas Hegi stated its absence from both these continents.

bescens to a subspecies, *M. spicatum* subsp. *exalbescens* Hult., because ". . . the difference between the types is . . . so small that I prefer to regard *M. exalbescens* as a geographical race of *M. spicatum*." Finally, Fernald (1919), in his citations of collections, notes some Colorado material with unusually elongate bracts, a condition relating more to *M. spicatum* than to his species.

In Figure 1 the approximate locations of those citations above which appear to be in dispute with Fernald's separation are denoted as circles on this continent. It is obvious that these points lie in areas which can be considered peripheral in relation to the whole range of *M. exalbescens*.

To attest further to the variability of *M. spicatum*, one needs only to consult European floras such as that of Hegi for a list of several varieties. Indeed, Lange (1887) described one, *M. spicatum* var. *capillaceum* Lange, for Greenland which is quite adjacent to the range of *M. exalbescens*. It is unfortunate that this work was not readily available for comparison with the species considered earlier, especially since Fernald cited a specimen of *M. exalbescens* from Greenland (1919, p. 120).

To further support the implied variability of the complex, sheets from the collections at the New York Botanical Gardens were examined. The number of pairs of leaf divisions and stem color were given emphasis since other characteristics do not show well in the dried material. Three specimens labeled *M. spicatum* var. *exalbescens* Jeps. were examined: 1) No. 1402, 1477. 1941. A. H. Holmgren, Nevada. 2) No. 4910. 1939. C. L. Hitchcock, Oregon (Deschutes River). 3) No. 5139. 1939. I. W. Clokey, California (Lake Arrowhead). These specimens could not be separated from *M. exalbescens* Fern. by superficial characters.

Three specimens of Scandinavian material were examined: 1) 1869. Prof. Boeck, Norway; labeled simply "Myriophyllum" (placed in *M. spicatum* file). This specimen resembled *M. exalbescens* in every superficial character: whitened stem, short floral bracts and 6–8 pairs of leaf segments. 2) No. 823. 1913. E. of Hälström, Sweden (Lake Torankijärvi); labeled *M. spicatum;* possessed whitened stem and 6–7 pairs of leaf divisions. 3) 1882. Thedensis, Sweden (Stockholm); whitened stem and 8–10 pairs of leaf segments.

Ten specimens of far-eastern material were examined: 1) No. 18420. 1928. China (Univ. of Nanking); labeled *M. spicatum;* fulvous stem and 16–21 pairs of leaf divisions. 2) No. 807. 1933. China; whitened stem, elongate pistillate bracts, up to 27 pairs of leaf divisions. 3) No. 3337. 1903. Leg. D. Litvinov, Manchuria (Sangari River); labeled *M. verticillatum* because of prominent elongate lowermost bracts; specimen the precise image of Series I material from New Jersey. 4) No. 3412. 1902. Litvinov, west. Manchuria (Sta. Chingis-Khan); label and characteristics same as above specimen. 5) No. 9669. 1936. W. Koelz, India (Shigar, Baltistan); labeled *M. spicatum;* two specimens duplicating those of N. J. Series I. 6) No. 8959. 1936. India (Dal Lake in northwestern Himalayas, Srinagar, Kashmir); labeled *M. spicatum;* characters same as sheet above. 7) No. 6752a. 1922; 8) No. 399a. 1913; 9) No. 10205a. 1929. All three by R. R. Stewart, Dal Lake; characters same as No. 8959 above. 10) No. 895. 1927. U.S.S.R.; labeled *M. spicatum;* characterized by whitened stem and only up to eight pairs of leaf divisions. Additional material examined from the interior of Eurasia showed no variation from typical *M. spicatum.*

These sheets indicate for the most part an *M. exalbescens* influence in both Scandinavia and the Far East, both of which regions are peripheral in relation to the whole distribution of *M. spicatum.* The approximate locations of the above collection sites appear in Figure 1 as circles on the Eurasian continent.

The distribution of *all* the circles in the figure suggests definite intergrade areas between *M. spicatum* and *M. exalbescens.* Thus the third hypothesis appears to be fairly well substantiated and there is indicated a variable circumboreal complex which it seems desirable to treat nomenclaturally as a single species.

It would not seem expedient to carry the present classification since this necessitates the naming of all the kinds of intergrades which might occur, a task with plural limitations. There exists a possibility that *M. exalbescens* Fern. and *M. spicatum* var. *capillaceum* Lange are the same since both of these descriptions were based, in part only in the former instance, upon material from Greenland. This would invalidate Fernald's name in the varietal category through precedence. However, the results of this study indicate a subspecific rank for this taxon and the

name may be written *M. spicatum* subsp. *exalbescens* (Fern.) Hult. Intergrades can then be referred to this taxon or to *M. spicatum* L., depending upon which a particular collection more nearly resembles. Excluding from consideration Eurasian variations which may already have been treated but which the writer is in no position to discuss, the Series I American material and the far-eastern intergrade material belong, under this classification, to *M. spicatum* L. The Series II material, other American material, and probably also the Scandinavian intergrades are to be taken as *M. spicatum* subsp. *exalbescens* (Fern.) Hult.

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Sheets of the New Jersey material analyzed in the study are filed in the Chrysler Herbarium at Rutgers University.

Summary

1. This study was undertaken because of the discovery that some of the material of *M. exalbescens* Fern. bore a superficial resemblance to the Eurasian counterpart, *M. spicatum* L.

2. The descriptions of four species are provided 1) to indicate their close similarity, 2) to emphasize the variable nature of the group in general, and 3) possibly to question several of the descriptions.

3. Two series of New Jersey material, one resembling typical *M. exalbescens* and the other *M. spicatum*, were compared to determine their relation to one another and to the two species which they resembled. They were indicated to be intermediate between these species.

4. Three hypotheses were propounded to explain this intergradation. The one selected as best-supported was based upon evidence favoring the consideration that *M. exalbescens* is a geographical variant of a circumboreal *M. spicatum* complex.

5. Due to the indicated probability of widespread intergradation, it was deemed advisable hereafter to consider *M. exalbescens* Fern. as a subspecies, *M. spicatum* subsp. *exalbescens* (Fern.) Hult.

6. Thus both *M. spicatum* L. and *M. spicatum* subsp. *exalbescens* Hult. go on record for New Jersey, the record for the former being a new one.—Botany Department, Rutgers University, New Brunswick, New Jersey.

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